Restorations of the Head of *Osteolepis*.

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(With 6 Text-figures.)

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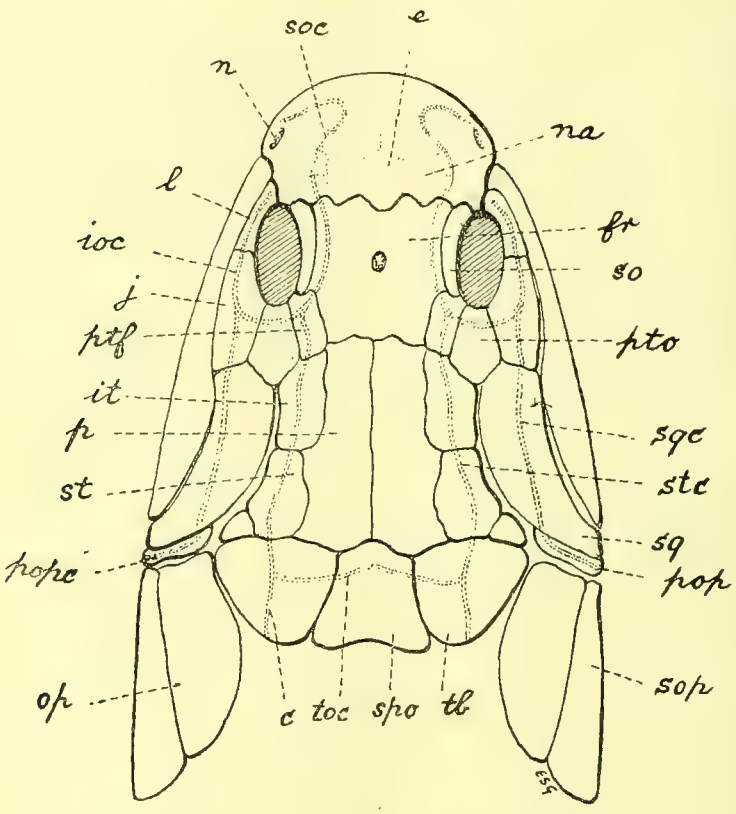
The genus *Osteolepis* is one of the commonest and best-known of the early Devonian Teleostomes. Nevertheless the exact disposition and homology of the superficial bones of the head are still but imperfectly understood. Two recently published restorations of the head, one by Gregory (**6**) and the other by Watson and Day (**14**), differ so remarkably from each other that it seemed advisable to reinvestigate the subject; for the Osteolepidæ are a very interesting and important group. In many respects, as for instance in the form of the paired fins and in the cosmoid structure of the scales, they approach the Devonian Dipnoi such as *Dipterus* (Goodrich, **4**, **5**); while, on the other hand, the skull shows undoubted affinity with the early Amphibia (Stegocephali). Huxley, I think unfortunately, in his valuable work on the fishes of the Devonian epoch (**7**), included *Osteolepis* and its fossil relatives together with *Polypterus* in the one group Crossopterygii. *Polypterus*, however, as I have endeavoured to show elsewhere (**5**), really differs fundamentally in its structure from the Osteolepids, and is almost certainly an aberrant Actinopterygian preserving some primitive characters. But, however this may be, there can be little doubt that the Osteolepidæ have departed less from the structure of the common ancestor of the Teleostomi and Tetrapoda than any other known fish. A thorough understanding of the structure of the skull of *Osteolepis* is, therefore, of the greatest importance for the elucidation of the homologies of the bones in the higher Vertebrates.

The most complete restorations of the skull of *Osteolepis* yet published are those given by Pander in his well-known monograph (**10**). But, beautiful as are his figures and excellent his reconstructions, they can by no means be trusted in every detail. Since then, Traquair has contributed a very good restoration of the whole fish (**13**), without detailed figures of the head; and Smith Woodward in his text-book (**15**) has given a figure of the roof of the skull, which is in all essentials correct. As already mentioned above, in his interesting discussion of the origin of the Tetrapoda (**6**) W. K. Gregory has figured restorations of *Osteolepis microlepidotus*, admittedly based on Pander's work; while D. M. S. Watson and H. Day, in their valuable paper on "Palæozoic Fishes" (**14**), restore *Osteolepis macrolepidotus*. Three sets of these figures from Pander, Gregory, and Watson & Day are here reproduced for comparison (figs. 2, 3, 4, & 5).

For my own restorations (figs. 1 A & B) I have not only had the benefit of the work of my predecessors, but have been able to study a large number of excellent specimens in various collections. I have to thank the authorities of the Museum of Practical Geology, Jermyn Street, for affording me every facility for the study of the fine series in their keeping, also Prof. Sollas for the loan of specimens in the Geological Department of the Oxford

Fig. 1 A.



Restoration of the head of *Osteolepis macrolepidotus*, Ag.

Dorsal view, enlarged.

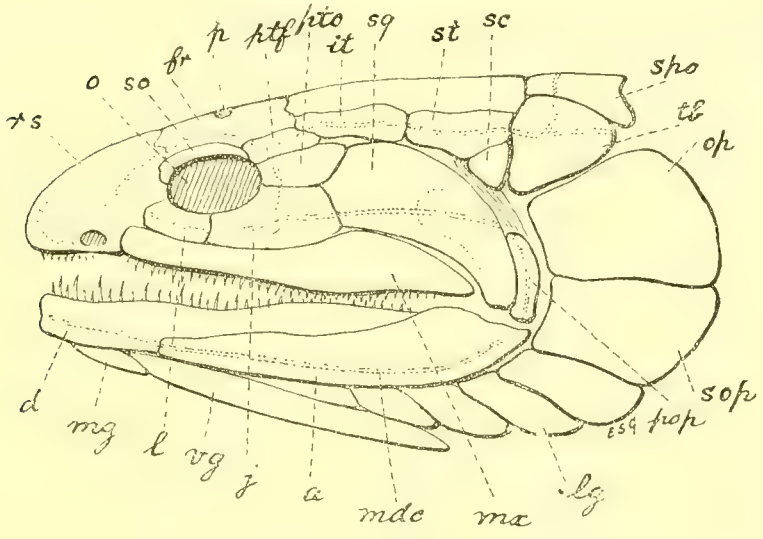
(For lettering see fig. 1 B.)

University Museum; but more especially Dr. A. Smith Woodward for his unfailing kindness and helpfulness during my frequent visits to the British Museum of Natural History.

As for the general disposition of the skull-plates covered with cosmine the figures speak for themselves, and only certain points of doubt or disagreement need be discussed in detail. First of all it may be mentioned that,

although my restorations apply more particularly to *O. macrolepidotus*, yet I find no important difference between that species and *O. microlepidotus*. The most careful scrutiny has convinced me that the supposed transverse series of small plates behind the parietals figured in *O. microlepidotus* by Pander, and accepted by Gregory, are not separate elements. They are parts of the supratemporals and parietals, and the often incomplete lines

Fig. 1 B.



Restoration of the head of *Osteolepis macrolepidotus*, Ag.

Left side view.

a, angular; *c*, main lateral-line canal; *d*, dentary; *e*, ethmoid included in rostral shield; *fr*, frontals fused in middle line and enclosing the pineal opening; *ioc*, infra-orbital canal; *it*, intertemporal; *j*, jugal; *l*, lacrymal; *lg*, lateral gular; *mdc*, mandibular canal; *mg*, median gular; *mx*, maxilla; *n*, nostril; *na*, nasal included in rostral shield; *o*, orbit; *op*, opercular; *p*, pineal opening; *pop*, preopercular; *popc*, preopercular canal; *ptf*, postfrontal; *pto*, postorbital; *rs*, rostral shield; *sc*, scale-like plate overhanging hyo-mandibular; *so*, supraorbital; *soc*, supraorbital canal; *sop*, subopercular; *spo*, dermal supraoccipital or postparietal; *sq*, squamosal; *sqc*, squamosal canal; *st*, supratemporal or pterotic; *stc*, supratemporal canal; *tb*, tabulare; *toc*, transverse occipital canal; *vg*, ventral paired gular.

which were supposed to be sutures marking them off from these bones are merely superficial grooves involving only the cosmine layer, and possibly indicating the presence of rows of small pit-organs or some other sensory structures. I can find no evidence of the existence of such a transverse series in any other Osteolepid; and an examination of the under surface

shows in this region the bone stretching uninterruptedly from three centres of ossification on each side, and three only : the parietal, the intertemporal, and the supratemporal. Grooves similar to those just mentioned are found on the frontals, diverging from the hinder border (as figured by Pander, see fig. 5), on the squamosal, and on some of the trunk scales running between the lateral-line scales and the mid-dorsal line. The diverging lines on the frontals do not mark off the postfrontals as suggested by Gregory; these bones are distinct but small, harbour the lateral-line canal, and seem just to reach the edge of the orbit. A distinct intertemporal is present. A suture separates the two parietals; but the frontals are fused superficially, although the suture can be distinguished on the inner surface. In one specimen a small plate and a minute nodule, possibly transparent in the living, were situated in the pineal foramen. Jaekel figures several such plates in *Diplopterus* (**8**). In front of the frontals the snout is covered by a shield formed of small plates the outlines of which can still be distinguished

FIG. 2.

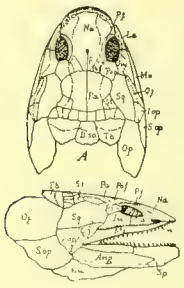


FIG. 3.

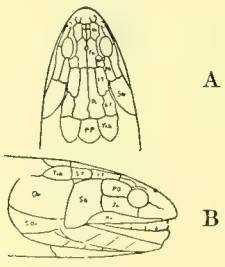


Fig. 2. Restoration of the dorsal, A, and right side, B, of the head of *Osteolepis microlepidotus*, Ag., from Gregory (**6**).

Fig. 3. Restoration of the dorsal, A, and right side, B, of the head of *Osteolepis macrolepidotus*, Ag., from Watson & Day (**14**).

Lettering for figs. 2 & 3:—

D, dentary; *D.So.*, dermal supraoccipital; *F* & *Fr*, frontals; *Gu*, gular; *I.op.*, interopercular; *It*, intertemporal; *Ju*, jugal; *La*, lacrymal; *Mx*, maxilla; *n*, nostril; *NA*, nasal; *OP*, opercular; *PA*, parietal; *Pf*, prefrontal; *P.O.* & *Po.O.*, postorbital; *Po.Fr.* & *Po.f.*, postfrontal; *P.P.*, postparietal; *Q.j.*, quadratojugal; *Sp*, splenial; *Sq*, squamosal; *S.OP.*, subopercular; *S.T*, supratemporal; *TAB* & *Tb*, tabulare.

to some extent on the inner surface. Unlike Watson and Day, I find here a fairly large median ethmoid between the nasals. Almost at the extreme lateral edge of the rounded rostrum can usually be seen an external nostril, which in some specimens is certainly surrounded by bone; while the position of the lower or posterior nostril is perhaps indicated by a notch on the

recurved ventral border of the shield. At the hinder corner of the skull, between the squamosal, tabulare and supratemporal, is a small triangular plate, figured by Pander and Gregory but not by Watson and Day. This scale-like plate seems to have been attached to the supratemporal and possibly overhung a spiracular opening. Below it passed the head of the large curved hyomandibular (traces of which can often be seen) to articulate with the supratemporal.

The lateral aspect of the head is by far the most difficult to interpret since the bones are here almost always much crushed and displaced, especially near the articulation of the jaws. Nevertheless, there can be no doubt of the existence of a large curved squamosal covering the whole of the cheek behind the postorbital and jugal. It has been well figured by Watson and Day, but Pander seems to have considered that it consisted of three plates, being partly misled by the curved superficial groove shown in figure 1 B. The squamosal reaches down to the articulation of the jaws, covering the quadrate region. Just behind its hinder edge, and overlying the end of the hyomandibular, is a small plate, the preopercular. This element is not figured by Watson and Day, but is possibly the one drawn by Pander and designated quadratojugal

Fig. 4. Fig. 5.

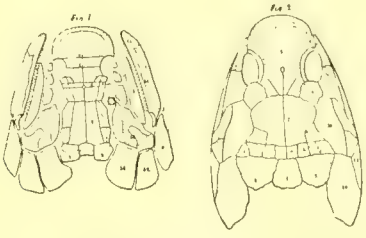


Fig. 4. Diagram of the bones of the skull of *Osteolepis macrolepidotus*, from Pander.
Fig. 5. Restoration of head of *Osteolepis microlepidotus*, from Pander.

by Gregory. If so, its true position has not been correctly determined by these authors. For a long time I doubted the existence of this separate element which is almost always considerably displaced; but after very careful examination of the most favourable material was finally convinced of its presence. The conspicuous large opercular bones pass ventrally into a series of lateral gular or bramchiostegal plates, which end in a pointed anterior element wedged in between the ventral gular and the lower jaw. Pander's restoration of the lower jaw appears to me much more correct than that of Watson and Day. No trace could be found of the series of infradentaries figured by the latter authors. The dentary and angular are obvious; an 'opercular' or prearticular plate seems to have covered part of the inner

surface, while further forward there are indications of a splenial showing on the lower outer surface. Of the existence of this element, however, I could not make certain.

Special attention was devoted to the course of the lateral-line system. It is not included in the figures of Watson and Day; but Pander studied it with considerable success. Recently it has again been figured by Collinge (3) without, however, adding much to Pander's results. These authors seem to have indicated in their restorations the distribution of the lateral-line pores rather than of the canal itself. The distribution of the two is by no means always the same, since the pores often stray far from the canal with which they are connected by delicate branches, and may be dotted about somewhat irregularly. The double broken line in my figures indicates the course of the canals only, as they are often beautifully revealed in the fossils.

The main lateral-line canal passing from the body scales enters the hinder region of the tabulare (often called supratemporal), runs forward through the supratemporal (pterotic), intertemporal, and postfrontal. About the middle of the tabulare it gives off a transverse occipital branch which joins its fellow from the opposite side in the median dermal supraoccipital (postparietal). That portion of the canal which lies between the origin of the transverse occipital and the origin of the infraorbital branch may be called the temporal canal. It is generally considered to belong to the infraorbital. In the postfrontal the canal branches into an upper supraorbital and a lower infraorbital canal. The former proceeds along the margin of the frontal to the rostral shield, where it describes an elegant curve and appears to end close to the nostril. I could find no anterior commissure; if such exists it must be on the ventral surface of the snout. The hitherto unrecognized junction of the supraorbital canal in the postfrontal bone with the infraorbital canal which runs up through the postorbital from the jugal I have been able to trace quite clearly. In the jugal a horizontal branch is given off from the infraorbital canal; it passes backwards across the squamosal, and apparently joins the preopercular canal which enters the angular, and proceeds forwards to the front end of the dentary.

These lateral-line canals are of special importance when comparing the skull of fishes with that of the primitive Tetrapoda. Pollard (11), Baur (2), Allis (1), and especially Moodie (9), have already made use of the canals in *Amia* and *Polypterus* in comparison with the Stegocephali, where the course of the lateral line is often marked by grooves. But these modern fish are specialized in many respects, and the pattern of *Osteolepis* agrees more closely with the Stegocephalian (see Moodie's figures, 9). However, it is not proposed to enter into a detailed discussion of the comparison in this paper, but it may be pointed out that the horizontal squamosal canal mentioned above is characteristic also of the Stegocephali. It is possibly

represented by the 'hyomandibular canal' of Selachians. A further study of this region in the Stegocephali might enable us to determine the homology of the lateral bones of the skull, especially of the quadratojugal, which is still very obscure. Judging from modern forms, the preopercular canal must have been supplied by a postspiracular branch of the hyomandibular nerve; we should not, therefore, expect to find it and the bone containing it in the skull of an Amphibian. Although a canal is known to have been present in the lower jaw of some Stegocephalians, its connexion with the more dorsal canals does not seem to have been made out. The settlement of this important point might help us to determine whether the preopercular is really represented in the Amphibian skull or not.

In conclusion attention may be drawn to the remarkable uniformity in the structure of the skull among the Osteolepidæ. *Thursius*, *Diplopterus*, and even *Megalichthys* seem to differ in no important respect from *Osteolepis* in the number and disposition of the bones on the head. The Rhizodontidæ also closely resemble the Osteolepids; and, except for the presence of infradentaries and for the subdivision of the squamosal, the restorations of *Rhizodopsis* made by Traquair (12), that most accurate of observers, would serve almost equally well for *Osteolepis*, as may easily be seen by comparing his figures with mine.

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